

On *Leptobrachium* from Thailand with a Description of a New Species (Anura: Pelobatidae)

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Abstract: We compared morphological characters among Thai populations of *Leptobrachium* currently assigned to *L. hasseltii* or *L. pullum*. We also examined syntypes of the latter, which was first described from Vietnam as *Megalophrys hasseltii* var. *pullus* Smith, 1921, and designated the lectotype. The Thai populations are slightly variable in adult and larval morphology, but are collectively different from *L. hasseltii* (originally described from Java) or *L. pullum*. We therefore describe a new species, *L. smithi*, for those populations on the basis of the sample from Khao Chong, southern Thailand.

Key words: Pelobatidae; *Leptobrachium*; Systematics; Thailand; Biogeography

The genus *Leptobrachium* (sensu stricto [not of Dubois, 1980] = subgenus *Leptobrachium* of Dubois and Ohler, 1998) is a group of pelobatid frogs characterized by a stocky body with slender, short hindlimbs (Inger and Stuebing, 1997; more detailed diagnosis in Dubois and Ohler, 1998). It occurs from southern China to the Philippines, Indonesia and the Sunda Is. to Bali (Frost, 1985). The type species of this genus, *L. hasseltii*, has long been regarded as widely distributed throughout the range of the genus (e.g., Taylor, 1962; Inger, 1966), although most of the previous authors surmised this apparently heterogeneous species to be a composite of several forms. Taylor (1962), for example, suggested occurrences of distinct forms within Thailand. Few authors, however, seriously studied these taxonomically problematic frogs until recently (detailed review in Dubois and Ohler, 1998).

Inger (1983), following personal information from Julian Dring, adopted the name *L. pullum* for the population from southern Thailand, and Dubois and Ohler (1998) also tentatively referred to populations from Thailand, as well as from Myanmar and Vietnam by this name. *Leptobrachium pullum* was originally described by Smith (1921) as *Megalophrys hasseltii* var. *pullus* from Arbre Broyé, Langbian Plateau, Southern Annam (Vietnam). Smith (1921: 423) reported that the upper half of the iris of this species in life is scarlet. Recent recognition of the Thai populations as *L. pullum* probably relies on this iris color, which Zhao and Adler (1993, as *L. hasseltii*: commented by Matsui and Ota, 1995:

239) and Manthey and Grossmann (1997) clearly presented through photographs of individuals from western and northeastern Thailand, respectively.

However, Smith (1921) also clearly indicated that he split *M. h.* var. *pullus* from “typical *hasseltii*” from Siam (=Thailand) and the Malay Peninsula on the basis of the differences in body shape and coloration. Because he is famous for his very active surveys throughout Thailand (e.g., Smith, 1922) and must have been very familiar with *Leptobrachium* from this country, the above statement by him deserves special attention. The current taxonomic arrangement of applying the name of *L. pullum* to the Thai populations simply on the basis of similar eye color is logically problematic. Nevertheless, very few recent authors have actually compared the Thai populations of *Leptobrachium* with the typical *L. pullum* in detail (e.g., Inger et al., 1999).

During our five years’ field survey of many places in Thailand, we observed a number of adult and larval specimens of *Leptobrachium* in life and recorded their calls. One of us (MM) also examined syntypes of *Megalophrys hasseltii* var. *pullus* Smith, 1921 (= *Leptobrachium pullum*) stored at the Natural History Museum, U. K. (BM) and of *Leptobrachium hasseltii* kept at the Museum of Natural History at Leiden (RMNH).

In this paper, we analyze variations among the Thai populations and also compare them morphologically with syntypes of *L. pullum* and *L. hasseltii*. As a result, we describe a new species from Khao Chong, southern Thailand.

MATERIALS AND METHODS

Extensive field surveys were made throughout Thailand between September of 1993 and September of 1997 (Fig. 1). We collected specimens, fixed them in 10% formalin, and later stored them in 70% ethanol. Whenever possible, we recorded calls using a cassette tape recorder (Sony TC-D5) with an external microphone (Sony ECM-23), and later analyzed them using computer programs, SoundEdit Vers. 2 and SoundEdit Pro (MacroMind-Paracomp, Inc.) on a Macintosh computer. Terminology for acoustic characteristics follows Matsui (1997).

For all preserved adult specimens, we took the following eight body measurements following Matsui (1984): 1) snout-vent length (SVL); 2) head length (HL); 3) head width (HW); 4) lower arm length (LAL); 5) tibia length (TL); 6) foot length (FL); 7) hindlimb length (HLL); 8) inner metatarsal tubercle length (IMTL). All measurements were made to the nearest 0.1 mm with a dial caliper under a binocular dissecting microscope. Larvae were assigned to developmental stages following Gosner (1960) and measured following Matsui (1979).

Variation in SVL was examined by analysis-of-variance (ANOVA) with the Tukey range test. Each of the other characters was converted to a percentage ratio (R) in relation to SVL and statistical comparisons were made among populations with a sample size of four or larger when males and females were combined. For these variables, Kruskal-Wallis tests with nonparametric multiple comparisons or Mann-Whitney U tests were performed to detect the presence or absence of differences in the frequency distributions. The significance level was set at 0.05.

RESULTS

Distribution of Leptobrachium in Thailand.—

From our field surveys, we confirmed the occurrences of *Leptobrachium* at the following localities: (1) Phu Luang, Loei Province, alt. 980 m; (2) Mae Hong Son, Mae Hong Son Province (at Pha Sua Waterfall, alt. 570 m); (3) Doi Suthep, Chiang Mai Province (at Montathan Waterfall, alt. 1000 m); (4) Doi Inthanon, Chiang Mai Province (at Ban Khun Klang, alt. 1350 m); (5) Sangkhla Buri, Kanchanaburi Province, alt. 540 m; (6) Erawan, Kanchanaburi Province, alt. 240 m; (7) Pilok, Kanchanaburi Province, alt. 620 m; (8) Pa Lao U, Phetchaburi Province, alt. 280 m; (9) Khlong Saen Wildlife Sanctuary, Surat Thani Province, alt. 130 m; (10) Khao Luang,

Nakhon Si Thammarat Province, alt. 370 m; (11) Khao Pra Taw, Phuket, Phuket Province, alt. 80 m; (12) Khao Chong, Trang Province (at Ton Nam Plu Waterfall, alt. 260 m, Ton Te Waterfall, alt. 210 m, and Sairung Waterfall, alt. 260 m). We could not find *Leptobrachium* in other parts of Thailand, notably in the eastern and central regions (Fig. 1).

Adult morphology.—In all specimens observed except one from Ban Khun Klang, Doi Inthanon, the upper half of the iris was scarlet, orange, or yellow. The exceptional individual with the upper half of the iris light sky blue was

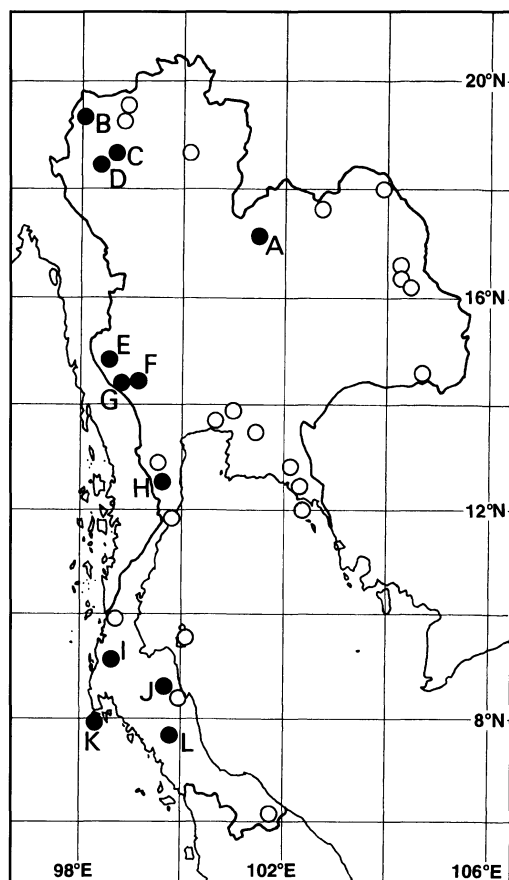


FIG. 1. Map of Thailand, showing sampling localities where specimens of *Leptobrachium* were sampled (closed circles) or not sampled (open circles). A: Phu Luang, Loei; B: Mae Hong Son, Mae Hong Son; C: Doi Suthep, Chiang Mai; D: Doi Inthanon, Chiang Mai; E: Sangkhla Buri, Kanchanaburi; F: Erawan, Kanchanaburi; G: Pilok, Kanchanaburi; H: Pa Lao U, Phetchaburi; I: Khlong Saen, Surat Thani; J: Khao Luang, Nakhon Si Thammarat; K: Phuket, Phuket; L: Khao Chong, Trang.

identified as *L. chapaense* (see Dubois and Ohler, 1998), and was excluded from the analyses. Of the remainder, the population from Khao Luang, Nakhon Si Thammarat had an iris with a yellow upper half, whereas the irises of the other populations were scarlet or orange dorsally. Of the two specimens collected at exactly the same locality in Pa Lao U, Phetchaburi Province, one had yellow and the other orange coloration in the upper half of the iris.

A summary of measurements is shown in Tables 1 and 2. No characters examined showed a definite geographic pattern of variation. The population sample of Erawan was the largest in male body size with a mean ($\pm$ SD) SVL of 60.0 ± 5.7 mm (Table 1), and that from Khao Chong was the smallest (mean $\pm$ SD= 41.4 ± 2.5 mm). The Erawan sample was significantly larger than all other samples in SVL ($p<0.05$), but the Khao Chong sample did not differ from several other samples. Of the remaining characters examined (Table 2), significant differences ($p<0.05$) among population samples were found only in RLAL and RHL. Samples from Nakhon Si Thammarat and Khao Chong had significantly larger RLAL (medians= 56.9% and 56.0% SVL, respectively) than samples from Erawan (50.8% SVL) and Mae Hong Son (51.8% SVL), and the sample from Nakhon Si Thammarat had larger RHL (127.7% SVL) than that from Mae Hong Son (118.0% SVL). No other combinations or characters yielded significant differences.

Body coloration was also variable, with the

TABLE 1. Morphometric variation in SVL (in mm) in *Leptobrachium* from Thailand and *L. pullum*.

Locality	Males			Females		
	N	$\bar{x}$	SD	N	$\bar{x}$	SD
Phu Luang	3	44.1	3.83 (39.8–47.2)	—		
Mae Hong Son	8	51.4	3.66 (47.4–57.5)	—		
Sangkhlha Buri	2	48.1	— (42.6–53.6)	—		
Erawan	7	60.0	5.69 (51.8–68.2)	1	78.0	—
Pilok	1	45.8	—	—		
Pa Lao U	1	58.3	—	1	73.3	—
Nakhon Si Thammarat	3	48.1	0.70 (47.4–48.8)	2	62.2	— (56.9–67.5)
Khao Chong	17	41.4	2.49 (36.2–46.1)	2	55.6	— (50.2–60.9)
<i>L. pullum</i>	6	45.5	1.18 (44.4–47.0)	2	51.1	— (49.4–52.8)

TABLE 2. Morphometric variation in relative values of each character to SVL (medians in % with ranges in parentheses) in *Leptobrachium* from Thailand and *L. pullum*. Males and females combined.

Locality	N	RHW	RHL	RLAL	RTL	RFL	RHLL	RIMTL	FL/TL
Phu Luang	3	42.0 (39.2–45.2)	42.4 (42.0–47.6)	52.7 (52.5–53.3)	35.6 (33.9–35.7)	31.9 (31.4–33.9)	118.2 (117.3–121.1)	3.9 (3.70–4.07)	0.94 (0.88–0.95)
Mae Hong Son	8	42.8 (40.2–45.1)	42.8 (40.9–46.0)	51.8 (49.5–55.5)	35.4 (34.4–37.7)	31.9 (31.1–36.2)	118.0 (116.4–124.0)	3.5 (3.06–4.31)	0.91 (0.87–0.96)
Sangkhlha Buri	2	43.8 (43.4–44.2)	44.5 (43.9–45.2)	48.7 (46.3–51.2)	36.3 (36.0–36.6)	33.5 (33.2–33.8)	118.2 (115.5–121.0)	3.9 (3.52–4.33)	0.92 (0.92)
Erawan	8	43.1 (41.4–44.4)	44.5 (42.3–45.6)	50.8 (47.0–53.7)	35.3 (32.6–36.7)	31.3 (29.9–34.5)	120.6 (109.6–127.0)	3.2 (2.89–3.95)	0.92 (0.83–0.96)
Pilok	1	41.9	43.9	51.2	36.5	33.0	122.7	2.8	0.90
Pa Lao U	2	44.4 (43.9–44.8)	44.5 (43.8–45.1)	51.7 (50.3–53.2)	36.0 (35.9–36.2)	31.2 (31.0–31.4)	118.6 (118.2–119.0)	3.2 (2.78–3.62)	0.87 (0.86–0.87)
Nakhon Si Thammarat	5	44.9 (43.7–46.2)	44.7 (43.7–45.0)	56.9 (55.5–61.2)	37.8 (36.5–40.3)	34.0 (32.1–37.1)	127.7 (126.2–131.8)	3.3 (2.94–3.53)	0.90 (0.85–0.93)
Khao Chong	19	44.3 (41.2–46.0)	44.9 (43.1–45.8)	56.0 (52.2–57.8)	36.5 (34.0–38.6)	33.3 (30.4–36.1)	123.9 (115.5–132.8)	3.5 (2.78–4.03)	0.91 (0.82–0.95)
<i>L. pullum</i>	8	41.5 (38.3–42.9)	41.1 (39.0–43.0)	48.7 (45.9–53.8)	32.3 (31.2–34.0)	34.7 (33.3–36.0)	113.0 (108.6–119.8)	4.9 (4.51–5.06)	1.05 (1.03–1.11)

ground color of the dorsum varying from gray to dark purplish brown. Most specimens from Erawan had a white ventrum with dark markings only on the chin and around the groin, whereas the ventral sides of specimens from other localities were white with varying amounts of darker infusion.

Tadpoles.—We were able to find tadpoles of *Leptobrachium* only in the southern localities (Pilok, Khao Chong, and Phuket). Larvae from these three localities were similar in color pattern to that described by Inger (1983) for the larvae tentatively assigned to *L. pullum* from Nakkon Si Thammarat. They were light brown in ground color with many small, irregular dark spots dorsally. There was a light area which was bounded by two dark bands or spots over the root of the tail. They also had dark spots on the sides of the tail, but lacked spots on the ventral surfaces of the head and body. The dental formula varied ontogenetically (cf. Matsui, 1979: 308), but in mature tadpoles (stages 26–37) from Khao Chong and Phuket, it was almost always $I:6+6/5+5:1$, while the formula was $I:5+5/5+5:1$ in those from Pilok. Although the small sample sizes prohibited exact comparisons, the Pilok population also seemed to have a slightly larger body than the remaining two populations; the total length of one tadpole of stage 31 was 63.0 mm in the Pilok sample, but 53.1 and 52.2 mm, respectively, in the Khao Chong and Phuket samples. Ventral glandular patches were absent in all populations.

Calls.—We recorded calls of *Leptobrachium* at Phu Luang, Doi Suthep, Mae Hong Son, Erawan, Khao Luang, and Khao Chong. Detailed comparisons of calls will be given elsewhere (Matsui, in preparation), but all populations were essentially similar in call characteristics. The calls consisted of a varying number (1–7) of notes each of which was composed of unclear pulses and lasted 100–600 msec. The dominant frequency was in the 600–1700 Hz range, with harmonics between 3000–8000 Hz, slight frequency modulation, and strong intensity modulation.

Comparisons with syntypes of *Megalophrys hasseltii* var. *pullus*.—Syntypes of *Megalophrys hasseltii* var. *pullus* Smith, 1921, are stored at BM and include six males and two females from two localities (see Appendix I). Although Smith (1921: 440) listed No. 2093 (now BM 1921.5.5.34) as a female, we identified it as a male. Because none of these specimens have been illustrated or nominated in any way, except for the type locality, there is no choice among

them in designating the lectotype other than choosing a specimen from the type locality designated by Smith (1921: 440). We hereby designate a male specimen BM 1921.5.5.36 (No. 5192 of Smith, 1921: 440) from Arbore Broyé as lectotype of *Megalophrys hasseltii* var. *pullus* Smith, 1921 (Fig. 5).

Smith (1921) noted that *M. h.* var. *pullus*

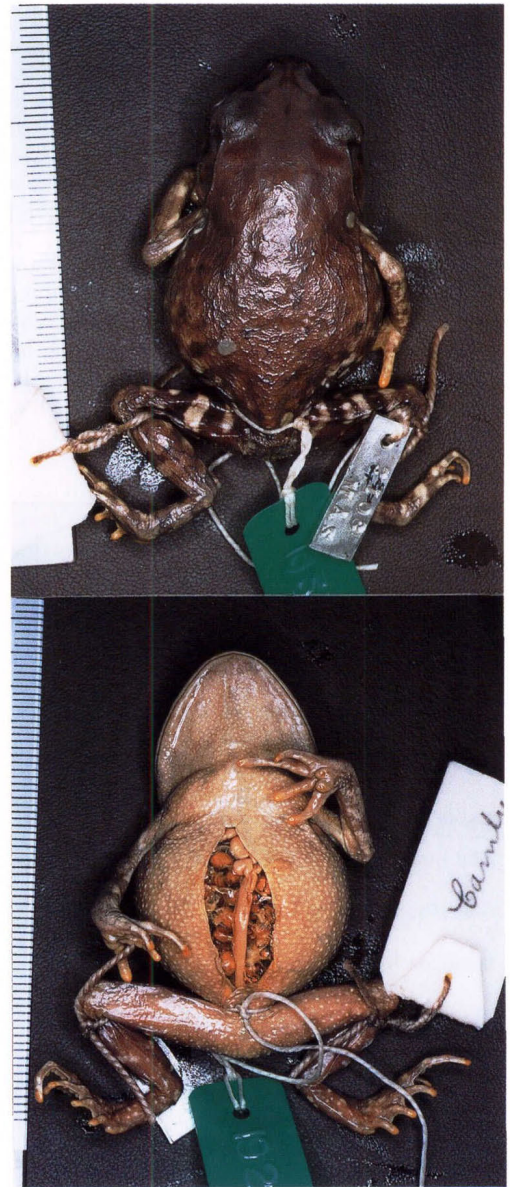


FIG. 2. Dorsal (top) and ventral (bottom) views of a paralectotype of *Leptobrachium pullum*. Female, BM. 1921.5.5.31 (No. 2108 of Smith, 1921).

(=*L. pullum*) differs from *M. hasseltii* from Thailand and Malaysia in its larger and more prominent metatarsal tubercle, longer leg, smaller size, and coloration. Of these, we confirmed the differences in size and shape of the inner metatarsal tubercle and body coloration, but not in the body size or leg proportion.

Leptobrachium pullum lacked ventral marking, unlike the Thai populations (see above). It also had distinct white spots on the lateral sides

of body, and the light bars on the tibia were also white (Fig. 2). Such coloration, similar to that in *L. chapaense* (as represented by a specimen in our collection: see above), was not seen in the Thai specimens in question. These white spots were usually on small to medium-sized warts, that were also absent in the Thai specimens.

Leptobrachium pullum also had a significantly larger inner metatarsal tubercle, relative to SVL (4.5–5.1% SVL, median=4.9%), than all the Thai specimens compared (medians=3.2–3.5% SVL; Fig. 5, Table 2). The shape of the inner metatarsal tubercle in *L. pullum* was more roundish and prominent than in the Thai specimens.

On the other hand, the body size of *L. pullum* (as represented by SVL, 44.4–47.0 [mean $\pm$ SD=45.5 $\pm$ 1.2] mm in six males and 49.4–52.8 [mean=51.1] mm in two females, according to our measurements) was within the range of the Thai specimens (see Table 1). In addition, contrary to the original description, *L. pullum* did not have significantly longer hindlimbs than the Thai specimens (Table 2). In contrast, the RHLL value was significantly smaller ($p < 0.05$) in *L. pullum* (median=113.0% SVL) than in samples from Nakon Si Thammarat and Khao Chong (127.7 and 123.9% SVL, respectively). In most of the Thai specimens, the tibiotarsal articulation reached the center of the tympanum, but it barely reached the posterior end of the tympanum in all specimens of *L. pullum* (Table 3).

Leptobrachium pullum had a longer foot, but shorter tibia, both relative to SVL, than some of the Thai specimens: In RTL *L. pullum* (median=32.3% SVL) was significantly smaller than samples from Nakon Si Thammarat (37.8% SVL) and Khao Chong (36.5% SVL), but was larger in RFL (34.7% SVL) than Erawan and Mae Hong Son samples (31.3 and 31.9% SVL, respectively). Thus the foot was longer than the tibia in *L. pullum*, but the situation was usually reversed in the Thai specimens, and the FL/TL ratio in *L. pullum* (median=1.05) was significantly larger than in all the populations compared from Thailand (medians=0.90–0.92). *Leptobrachium pullum* also differed from a few



FIG. 3. Dorsal (top) and ventral (bottom) views of the holotype of *Leptobrachium smithi*.



FIG. 4. Lateral view of larval *Leptobrachium smithi*.

population samples from Thailand in some other characters: *L. pullum* had significantly smaller RHL, RHW, and RLAL (medians=41.1, 41.5, and 48.7% SVL, respectively) than samples from Nakon Si Thammarat (44.7, 44.9, and 56.9% SVL, respectively) and Khao Chong (44.9, 44.3, and 56.0% SVL, respectively).

In this way, the populations of *Leptobrachium* from Thailand clearly differ from *L. pullum*, to which they have been assigned by most recent authors. Although slightly varying in a few external characters as above, they are collectively differentiated morphologically from all the congeneric, currently recognized species to a degree that is sufficiently great to be that of a distinct species. We therefore describe this form as follows:

Leptobrachium smithi sp. nov.

(Figs. 3, 5)

Megalophrys hasseltii: Smith, 1917, p. 23.

Megophrys hasselti hasselti: Taylor and Elbel, 1958, p. 1077, Fig. 14.

Leptobrachium hasseltii hasseltii: Taylor, 1962, p. 312, Figs. 11, 13.

Leptobrachium pullum: Inger, 1983, p. 15.

Holotype.—NHMT (National Science Museum of Thailand)-A 001, an adult male from Ton Nam Plu Waterfall, Khao Chong, Trang Province, Thailand (7°34' N, 99°49' E, alt. 260 m), collected on 16 January 1997 by Masafumi Matsui.

Paratypes.—NHMT-A 010 (1 male), CUZM (Chulalongkorn University, Museum of Zoology

(Am) 1999-5-8, 1-2 (2 males), KUHE (Graduate School of Human and Environmental Studies, Kyoto University) 23275, 23301, 23316-19, 23321-22, 23340-44 (13 males), KUHE 23302, 23345 (2 females), data same as the holotype.

Referred specimens.—KUHE, unnumbered: 10 tadpoles, data same as the holotype.

Diagnosis.—A moderate-sized form of the genus *Leptobrachium*; males 36-68 mm, females 50-78 mm SVL; upper half of iris scarlet or yellow, like *L. pullum*, but differing from it in the smaller size of inner metatarsal tubercle, less tuberculated dorsal skin, and lack of white spots on sides of body and on thigh.

Description of holotype.—Head broad and depressed, body tapering to groin; head length and width subequal; snout obtusely pointed, sharply sloping in profile, barely projecting beyond lower jaw; eye large and slightly projecting from sides of head, diameter slightly shorter than snout length; canthi sharp; lores oblique, moderately concave; nostrils lateral, below canthus, distinctly closer to tip of snout than to eye; internarial distance shorter than interorbital distance, latter wider than upper eyelid; no pineal spot; tympanum visible, diameter about three-fifths that of eye and separated from eye by two-thirds of tympanic diameter; vomerine teeth absent; tongue heart-shaped, notched posteriorly, without papillae; a median, subgular internal vocal sac in the mid-ventral line; oval vocal openings inside the corners of the mouth.

Forelimb slender; fingers moderately slender, unwebbed; first finger slightly longer than se-

TABLE 3. Variation in the point reached by the tibio-tarsal joint when the hindlimb is bent forwards along the body. Figures indicate the number of specimens (percentage frequency in parenthesis).

	Beyond anter. edge of tympanum	Between ant. and post. edge of tympanum	Behind post. edge of tympanum
Phu Luang			
Males	0	3 (100%)	0
Mae Hong Son			
Males	0	8 (100%)	0
Erawan			
Males	1 (14.3%)	5 (71.4%)	1 (14.3%)
Females	0	1 (100%)	0
Nakhon Si Thammarat			
Males	0	3 (100%)	0
Females	0	2 (100%)	0
Khao Chong			
Males	0	16 (94.1%)	1 (5.9%)
Females	0	2 (100%)	0
<i>L. pullum</i>			
Males	0	0	6 (100%)
Females	0	0	2 (100%)

cond, fourth shorter, third much longer; tips rounded, not swollen; inner palmar tubercle large, not extending onto first metacarpal and smaller outer palmar tubercle; subarticular tubercles indistinct, replaced by low callous tissue; nuptial pads absent.

Hindlimb slender and relatively short; heels do not meet when limbs are held at right angles to body; tibiotarsal articulation of adpressed limb reaching to the middle of tympanum; third toe longer than fifth; toe tips similar to those of fingers; webbing about half of toes, third toe with $3\frac{2}{3}$ phalanges free of web, fifth with $1\frac{1}{2}$ free (Fig. 5); inner metatarsal tubercle low, oval, length less than half distance between tip of first toe and tubercle; subarticular tubercles obscure, but elongate, replaced by low callous tissue.

Skin above nearly smooth, with minute granules scattered behind, especially around vent; ventrally granular; a low supratympanic ridge from eye to axilla; a round, flat gland at median border of axilla behind arm; a small, round femoral gland in distal half of posterior surface of thigh.

Color in alcohol.—Dark gray dorsally on head and body, with an irregular dark mark commencing discretely in frontal region and fading to half length of back; tympanum masked black dorsally; lips barred with black spots from below canthus and eye; sides with small dark spots; groin with dark spot extending onto anterior face of thigh; limbs marked dorsally with alternating grayish and dark brown crossbars, the darker ones much narrower on hindlimb; posterior face of thigh black with several white spots, continuous to bars across dorsal surface; ventrally white with varying

amounts of darker infusion, especially on throat and posterior half of abdomen.

Color in life.—Upper half of the iris was scarlet.

Measurements of holotype (in mm).—Measurements taken mostly following Matsui (1984: 236): SVL 41.2; HL 18.0 (43.7% SVL); N-EL 3.9 (9.5% SVL); SL 7.2 (17.5% SVL); EL 5.9 (14.3% SVL); T-EL 2.1 (5.1% SVL); TD 3.4 (8.3% SVL); HW 18.2 (44.2% SVL); IND 3.5 (8.5% SVL); ICD 7.4 (18.0% SVL); IOD 5.8 (14.1% SVL); UEW 4.5 (10.9% SVL); LAL 22.4 (54.4% SVL); IPTL 1.6 (3.9% SVL); HAL 9.5 (23.1% SVL); HLL 50.1 (121.6% SVL); TL 14.6 (35.4% SVL); FL 13.8 (33.5% SVL); first toe length 2.7 (6.6% SVL); IMTL 1.2 (2.9% SVL).

Variation.—Morphometric data are summarized in Table 1 together with those on the allied populations. The small sample size in females prohibits statistical comparisons, but snout-vent length of two females (mean = 55.6 mm) seems to be larger than that of two males (mean $\pm$ SD = 41.4 $\pm$ 2.5 mm). Otherwise, the two sexes seem to be nearly identical in body proportions (Table 1). Individuals vary slightly in coloration and pattern of markings, and many have a darker back with less prominent markings than in the holotype.

Tadpoles.—Body deep, ovoid; eyes dorsal, not visible from below; spiracle sinistral; anus dextral, opening at edge of ventral fin; tail muscle strong, fins beginning at root of tail; margin of dorsal fin convex, fin deeper than muscle beyond middle of tail; margin of ventral fin weakly convex, fin half depth of dorsal fin; tail tapering to rounded tip. Mouth ventral, subterminal; beaks heavy, coarsely serrate, black; labial teeth vary from I: 4+4/4+4: 1 to I: 6+6/5+5: 1 but I: 6+6/5+5: 1 in mature larvae; labial papillae thick; both clear lateral lines and ventral glandular patches absent. Light brown dorsally on head and body with many small, irregular dark spots; a light area bounded by two dark bands over root of tail; no spots on ventral surface of head and body; dark spots on anterior half of tail muscles, but no spots on tail fins (Fig. 4). Head and body from 14.2–19.7 mm and tail ratio to head and body 162–172% in tadpoles of stages 26–31.

Call.—The calls recorded at Khao Chong on 17 January 1997, at air temperatures of 23.0–24.4 C, consisted of one to seven (usually one) notes and lasted up to 2087 msec (Fig. 6). A note was composed of many unclear pulses and lasted from 109–230 msec. In a call with two or more notes, each note was emitted successively,

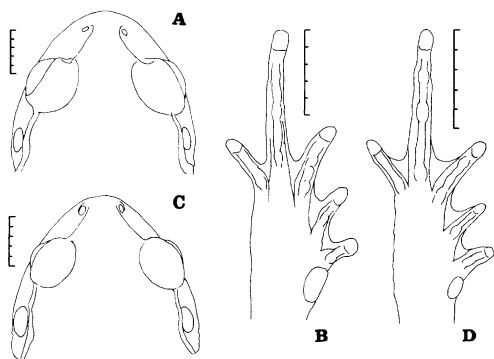


FIG. 5. Dorsal views of the head (A, C) and ventral views of the right foot (B, D) of the holotypes of *Leptobrachium pullum* (A, B; male, BM. 1921.5.5.36 (No. 5192 of Smith, 1921)) and *Leptobrachium smithi* (C, D). Scale indicates 5 mm.

with the note gap ranging from 279–477 msec and the note repetition rate 2.87–3.92 per sec. The dominant frequency was in the 750–1600 Hz range, and was more exactly about 950 and 1500 Hz. There were weak harmonics at about the 3000–4200 and 5800–7200 Hz ranges. Slight frequency modulation and strong intensity modulation were present.

Comparisons.—*Leptobrachium smithi* differs from the following congeneric species by the eye color: In *L. hainanense* (Liu et al., 1973; Ye et al., 1993), *L. chapaense* (Yang, 1991; Dubois and Ohler, 1998; Lathrop et al., 1998; our own observations), *L. xanthospilum*, and *L. banae* (Lathrop et al., 1998), the dorsal half of the iris is blue to white, although *L. chapaense* was originally described as having a dark iris (Bourret, 1937). *Leptobrachium nigrops* (Berry, 1975; our own observations), *L. montanum*, *L. abbotti* (Inger et al., 1995; our own observa-

tions), and *L. gunungense* (our own observations) have a black iris with or without a white ring surrounding the eyeball. The iris of *L. hasseltii* from the Sunda Islands including the type locality (Java) is reported to be red (Iskandar, 1998). Moreover, the species has many discrete dark markings dorsally (our own observations of the lectotype in BM; Dubois and Ohler, 1998: Fig. 4), unlike *L. smithi* whose dorsal dark markings are confluent. *Leptobrachium hasseltii* also has many small dark spots on the ventrum (our own observations of the lectotype). In addition, *L. hasseltii* has rows of ridges on dorsal surfaces of limbs that are absent in *L. smithi* (our own observations of the lectotype; see Iskandar, 1998: Photograph 3 top). Larval *L. hasseltii* have no dark markings (our own observations of specimens from Java in RMNH) quite dissimilar to *L. smithi* (see above description of tadpoles).

In contrast to the above species, *L. hendricksoni* from southernmost Thailand through Peninsular Malaysia to Borneo (Berry, 1975; our own observations) and *L. pullum* (Smith, 1921) is similar to *L. smithi* in sharing scarlet or yellow color in the dorsal half of the iris. However, *L. hendricksoni* has characteristic larvae that have many small dots on the body and tail unlike larval *L. smithi* which have a light body and tail with fewer but larger dark blotches. Adults of *L. hendricksoni* also have many small dots on the ventrum and are very easily distinguished from all other species except possibly for *L. hasseltii*. Although the tadpoles of *L. pullum* are unknown, the species differs from *L. smithi* in adult morphology as described above.

Range.—Thailand. Besides the type locality, Khao Chong, the specimens from the following localities were assigned to this species: Phu Luang (Loei Province), Doi Suthep (Chiang Mai Province), Mae Hong Son (Mae Hong Son Province), Sangkhla Buri, Pilok, and Erawan (Kanchanaburi Province), Pa Lao U (Phetchaburi Province), Khao Luang (Nakhon Si Thammarat Province), and Phuket (Phuket Province). Na Hao (Loei Province) and Doi Chiang Dao (Chiang Mai Province) (Taylor, 1962: see below). Also specimens reported from at least the southern region of Myanmar as *L. hasseltii* (e.g., Annandale, 1917) seem to belong to the present new species.

Natural history.—In Khao Chong, *L. smithi* was found in forests along mountain streams and near waterfalls. Many males began to call just after sunset from the forest floor apart from the water. Because of its cryptic coloration, it

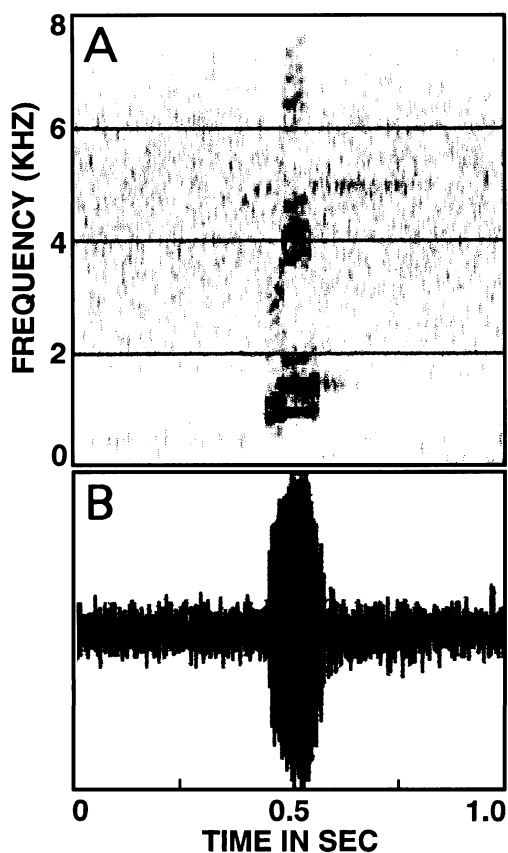


FIG. 6. Sonagram (A) and wave form (B) of the mating call of *Leptobrachium smithi* from Khao Chong, Thailand, recorded at an air temperature of 24.4°C.

was difficult to find them among dead leaves. Tadpoles of various sizes were found in the pools of streams in January.

Etymology.—The specific name is dedicated to Malcolm Smith who made great contributions to our understanding of the herpetofauna of Thailand and adjacent territories.

DISCUSSION

Annandale (1917) first discussed the possibility of distinct specific status for different local forms of the wide-ranging *Megalophrys* (= *Leptobrachium*) *hasseltii*. From the examination of tadpoles of this species, Annandale (1917) recognized three distinct color varieties (forms A–C); Of these, form A from the Malay Peninsula was described as having the whole body marked with small round black spots, and form B from Tenasserim (southern Myanmar) as dorsally and laterally spotted or blotched with a relatively small number of markings. According to Annandale (1917), form C from Java lacked dark spots or blotches. Slightly later, Smith (1917) noted that the tadpole of *M. hasseltii* from northern Thailand agreed with the form B of Annandale (1917). However, Annandale (1917), instead of according distinct specific status to these three forms, laid the greatest stress on the lack of correlations between body proportions and geographic distribution in these tadpoles.

From the current knowledge, the forms A and C of Annandale (1917) most likely correspond to *L. hendricksoni* from the Malay Peninsula (Taylor, 1962; our own observations), and the true *L. hasseltii* from Java and Bali (Iskandar, 1998), respectively. The coloration of the form B described by Annandale (1917) from Tenasserim, and additionally reported from northern Thailand by Smith (1917), conforms well to that of larval *L. smithi*.

Dubois and Ohler (1998) stressed the utility of the body size as a specifically diagnostic character of this genus, and suspected the presence of two species in Java on this ground. We, however, assume that the body size varies greatly between conspecific populations in *Leptobrachium*, and treat the great size difference of our Erawan and Khao Chong populations as an intraspecific variation. This is because no other tangible differences were found between these populations.

Now it is clear that at least three species of *Leptobrachium* occur in Thailand. *Leptobrachium chapaense* occurs in the high mountains of the northern region (Dubois and Ohler,

1998; our own observations). Although Inger et al. (1999) lumped this species with *L. pullum*, their data support our idea. By contrast, *L. hendricksoni* is limited to the lowlands of the extreme south (Taylor, 1962) and is more widely distributed in Peninsular Malaysia and Borneo (Berry, 1975; Inger and Stuebing, 1997). *Leptobrachium smithi* seems to occupy the inter-space between these two species both geographically and altitudinally.

Taylor (1962), showing photographs of four specimens from three different localities including Singapore, suggested the presence of two forms within Thailand. He noted that “the population from northwestern Siam probably merits subspecific designation.” He seems to have taken specimens from Loei (Fig. 11 in Taylor, 1962: 313) and Doi Chiang Dao (two specimens in Fig. 13 in Taylor, 1962: 315) as representatives of that population, which we can now identify as *L. smithi*. The remaining one from Singapore (Fig. 12 in Taylor, 1962: 314) surely belongs to *L. nigrops*, because of its slender body and distinct dorsal markings. In addition, no other congeneric species are known there (Lim and Lim, 1992). Taylor (1962), however, mentioned nothing about the distribution of this form within Thailand.

Inger (1983) noted an unnamed tadpole of this genus (*L. sp.*) from Doi Suthep. According to his description, *L. sp.* differs from *L. pullum* (= *L. smithi*) in color, besides the oral characteristics. *Leptobrachium sp.* lacks spots on the dorsum, unlike *L. pullum* which has many dark spots dorsally. We suspect *L. sp.* from Doi Suthep to be *L. chapaense*, but the larva of that species from Yunnan is reported to have markings on the root of the tail (Yang, 1991). Further field survey is necessary around Doi Suthep.

Dring (1979) showed the sonagram of a call of *L. hasseltii* from Trengganu, Malaysia. Although no detailed acoustic data are available, the sonagram resembles that of *L. smithi*. If this is the case, there may be also an altitudinal segregation of *L. smithi* and lowland *L. hendricksoni* within Malaysia as well. This type of segregation by height has been reported for *L. montanum* and *L. abbotti* in Borneo (Inger et al., 1995).

Manthey and Grossmann (1997) noted that the scarlet-colored area in the iris of *L. hendricksoni* varies from the whole iris to its upper half only. The color of the upper half of the iris actually varied between and even within a population in our sample. In extreme cases, the population from Phu Luang, Loei, had an iris

whose upper half was reddish orange in color, while in the population from Khao Luang, Nakhon Si Thammarat, the upper half of the iris was light yellow. We, however, have never observed an individual whose iris was dorsally sky blue except for an *L. chapaense* from a high altitude of Doi Inthanon. Although the eye color may vary intraspecifically to some extent, it seems a very important diagnostic character at the specific level in this genus. In fact, Inger et al. (1995) could differentiate two Bornean species by this character. A severe practical problem in identification is that the color does not last long in preservative.

As stated in comparisons, two recently described species of *Leptobrachium* from northern Vietnam (Lathrop et al., 1998), *L. chapaense* from northern Thailand, Vietnam and China (Yang, 1991; Dubois and Ohler, 1998; Lathrop et al., 1998), and *L. hainanense* from Hainan (Liu et al., 1973; Ye et al., 1993) have a dorsally sky blue iris. On the other hand, *Vibrissaphora*, a close relative of *Leptobrachium* (sensu stricto) and sometimes synonymized with it (Frost, 1985) or regarded as another subgenus of *Leptobrachium* (sensu lato: Dubois and Ohler, 1998), occurs in northern Vietnam and China. This genus includes some members with the iris sky blue or lime dorsally (Liu and Hu, 1961; Dubois and Ohler, 1998), but none have been reported to have an orange or scarlet iris. Therefore, the condition in the northern species of *Leptobrachium* (i.e., blue sky iris) seems to represent a primitive state in this genus (sensu stricto). Future phylogenetic analyses using various (e.g., molecular) techniques are necessary to elucidate the evolution of the eye color in this and allied genera.

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LITERATURE CITED

ANNANDALE, N. 1917. Zoological results of a tour in

- the Far East. Mem. Asiatic Soc. Bengal 6: 119–155+pl. 5–6.
- BERRY, P. Y. 1975. The Amphibian fauna of Peninsular Malaysia. Tropical Press, Kuala Lumpur. x+130 p.
- BOURRET, R. 1937. Notes herpétologiques sur l'Indochine Française XIV–XV. Annexe Bull. Gén. Instr. Publique, Hanoi 1937(4): 1–80.
- DRING, J. C. M. 1979. Amphibians and reptiles from northern Trengganu. Malaysia, with descriptions of two new geckos: *Cnemaspis* and *Cyrtodactylus*. Bull. Br. Mus. Nat. Hist. (Zool.) 34(5): 181–241.
- DUBOIS, A. 1980. Notes sur la systématique et la répartition des amphibiens anoures de Chine et des régions avoisinantes. IV. Classification générique et sous-générique des Pelobatidae Megophryinae. Bull. Mens. Soc. Linn. Lyon 49(8): 469–482.
- DUBOIS, A. AND A. OHLER. 1998. A new species of *Leptobrachium* (*Vibrissaphora*) from northern Vietnam, with a review of the taxonomy of the genus *Leptobrachium* (Pelobatidae, Megophryinae). Dumériliana 4(1): 1–32.
- FROST, D. R. (ed.). 1985. Amphibian Species of the World: A Taxonomic and Geographical Reference. Allen Press, Lawrence, Kansas. i+v+732 p.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.
- INGER, R. F. 1966. The systematics and zoogeography of the Amphibia of Borneo. Fieldiana: Zool. 52: 1–402.
- INGER, R. F. 1983. Larvae of Southeast Asian species of *Leptobrachium* and *Leptobrachella* (Anura: Pelobatidae). p. 13–32. In: A. G. J. Rhodin and K. Miyata (eds.), Advances in Herpetology and Evolutionary Biology. Mus. Comp. Zool., Cambridge, Massachusetts.
- INGER, R. F., N. ORLOV, AND I. DAREVSKY. 1999. Frogs of Vietnam: A report on new collections. Fieldiana: Zool. N. S. (92): 1–46.
- INGER, R. F. AND R. B. STUEBING. 1997. A Field Guide to the Frogs of Borneo. Nat. Hist. Publ. Sdn. Bhd., Kota Kinabalu. ix+205 p.
- INGER, R. F., R. B. STUEBING, AND F.-L. TAN. 1995. New species and new records of anurans from Borneo. Raffles Bull. Zool. 43: 115–131.
- ISKANDAR, D. T. 1998. The Amphibian of Java and Bali. Puslitbang Biologi, LIPI, Bogor. xvi+117 p.+26 pls. (in Indonesian)
- LATHROP, A., R. W. MURPHY, N. L. ORLOV, AND C. T. HO. 1998. Two new species of *Leptobrachium* (Anura: Megophryidae) from the central highlands of Vietnam with a redescription of *Leptobrachium chapaense*. Russian J. Herpetol. 5(1): 51–60.
- LIM, K. K. P. AND F. L. K. LIM. 1992. A Guide to the Amphibians & Reptiles of Singapore. Singapore Centre, Singapore. 160 p.
- LIU, C.-C. AND S.-C. HU. 1961. Chinese Tailless Batrachians. Science Press, Peking. xvi+364 p+28 pls. (in Chinese)

- LIU, C.-C., S.-C. HU, L. FEI, AND C.-C. HUANG. 1973. On collections of amphibians from Hainan Island. *Acta Zool. Sinica*. 19(4): 385–404. (in Chinese, with English abstract)
- MANTHEY, U. AND W. GROSSMANN. 1997. Amphibien und Reptilien Südostasiens. Natur und Tier Verlag, Münster. 512 p.
- MATSUI, M. 1979. Amphibians from Sabah I. Systematic and natural history notes. *Contr. Biol. Lab. Kyoto Univ.* 25(4): 303–346.
- MATSUI, M. 1984. Morphometric variation analyses and revision of the Japanese toads (Genus *Bufo*, Bufonidae). *Contr. Biol. Lab. Kyoto Univ.* 26(3/4): 209–428.
- MATSUI, M. 1997. Call characteristics of Malaysian *Leptolalax* with a description of two new species (Anura: Pelobatidae). *Copeia* 1997(1): 158–165.
- MATSUI, M. AND H. OTA. 1995. On Chinese herpetology. *Herpetologica* 51(2): 234–250.
- SMITH, M. A. 1917. A list of the batrachians at present known to inhabit Siam. *J. Nat. Hist. Soc. Siam* 2: 226–231.
- SMITH, M. A. 1921. New or little-known reptiles and batrachians from southern Annam (Indo-China). *Proc. Zool. Soc. London* 1921: 423–440 + pl. 1–2.
- SMITH, M. A. 1922. Notes on reptiles and batrachians from Siam and Indo-China, (No. 1). *J. Nat. Hist. Soc. Siam* 4: 203–214.
- TAYLOR, E. H. 1962. The amphibian fauna of Thailand. *Univ. Kansas Sci. Bull.* 63: 265–599.
- YANG, D.-T. (ed.). 1991. Amphibian-Fauna of Yunnan. China Forestry Publ. House, Beijing. iv + 259 p. (in Chinese)
- YE, C., L. FEI, AND S. HU. 1993. Rare and Economic Amphibians of China. Sichuan Publ. House of Sci. Technol., Chengdu. iii + 2 + 2 + 7 + 412 p. (in Chinese)
- ZHAO, E.-M. AND K. ADLER. 1993. Herpetology of China. SSAR, Oxford, Ohio. i-v + 522 p. + 48 pls.

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APPENDIX I.

Specimens examined.—The species and localities of samples used are given below. The samples are deposited at the Graduate School of Human and Environmental Studies, Kyoto University (KUHE), National Science Museum of Thailand (NHMT), Chulalongkorn University, Museum of Zoology (CUZM), Natural History Museum, U. K. (BM), and Museum of Natural History at Leiden (RMNH).

Leptobrachium smithi (N=48, all from Thailand):

Phu Luang, Loei Province, KUHE 19280–82; Mae Hong Son, Mae Hong Son Province, KUHE 19823, 19830–36; Sangkhla Buri, Kanchanaburi Province, KUHE 19518, 19538; Erawan, Kanchanaburi Province, KUHE 20000–03, 20031–32, 20059–60; Pilo, Kanchanaburi Province, KUHE 19939, 4 tadpoles KUHE unnumbered; Pa Lao U, Phetchaburi Province, KUHE 20200–01; Khao Luang, Nakhon Si Thammarat Province, KUHE 19392–95, 19399; Khao Pra Taw, Phuket, Phuket Province, 10 tadpoles KUHE unnumbered; Khao Chong, Trang Province, NHMT A 001, A 010, CUZM (Am) 1999–5–8, 1–2, KUHE 23275, 23301–02, 23316–19, 23321–22, 23340–45, 10 tadpoles KUHE unnumbered.

Leptobrachium chapaense (N=1, from Thailand): Doi Inthanon, Chiang Mai Province, KUHE 19122.

Leptobrachium pullum (N=8, from Vietnam: syntypes): Arbre Broyé, BM 1921.5.5.32–33 (No. 2090–2091 of Smith, 1921: 440), 1921.5.5.34 (No. 2093), 1921.5.5.35 (No. 2101), 1921.5.5.36 (No. 5192); Camly, BM 1921.5.5.29 (No. 2103), 1921.5.5.30 (No. 2105), 1921.5.5.31 (No. 2108).

Leptobrachium hasseltii (N=2, from Indonesia: syntypes): Java, RMNH 2015 (lectotype), 2014 (paralectotype).